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A Comparison of the Influences of Urbanization in Contrasting Environmental Settings on Stream Benthic Algal Assemblages

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Abstract.—Patterns of stream benthic algal assemblages along urbanization gradients were investigated in three metropolitan areas—Boston (BOS), Massachusetts; Birmingham (BIR), Alabama; and Salt Lake City (SLC), Utah. An index of urban intensity derived from socioeconomic, infrastructure, and land-use characteristics was used as a measure of urbanization. Of the various attributes of the algal assemblages, species composition changed along gradients of urban intensity in a more consistent manner than biomass or diversity. In urban streams, the relative abundance of pollution-tolerant species was often higher than in less affected streams. Shifts in assemblage composition were associated primarily with increased levels of conductivity, nutrients, and alterations in physical habitat. Water mineralization and nutrients were the most important determinants of assemblage composition in the BOS and SLC study areas; flow regime and grazers were key factors in the BIR study area. Species composition of algal assemblages differed significantly among geographic regions, and no particular algal taxa were found to be universal indicators of urbanization. Patterns in algal biomass and diversity along urban gradients varied among study areas, depending on local environmental conditions and habitat alteration. Biomass and diversity increased with urbanization in the BOS area, apparently because of increased nutrients, light, and flow stability in urban streams, which often are regulated by dams. Biomass and diversity decreased with urbanization in the BIR study area because of intensive fish grazing and less stable flow regime. In the SLC study area, correlations between algal biomass, diversity, and urban intensity were positive but weak. Thus, algal responses to urbanization differed considerably among the three study areas. We concluded that the wide range of responses of benthic algae to urbanization implied that tools for stream bioassessment must be region specific.

Introduction

Streams go through hydrological and water quality changes as they become part of the urban landscape (Paul and Meyer 2001). Alterations of stream habitat inevitably lead to transformations in stream biota, including algal assemblages. Although the presence of harmful chemicals in streams or the disappearance of important fish species attracts attention, changes in algal assemblages usually do not cause public concern

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unless excessive amounts of algae diminish the esthetic value of streams, clog water supplies, or cause secondary water pollution. Algae are sensitive, however, to water chemistry and habitat disturbance and, thus, have a long history of being used in water quality monitoring (Lowe and Pan 1996). Algae also play an important role in the function of stream ecosystems. Algae are a source of organic matter and provide habitat for other organisms, such as nonphotosynthetic bacteria, protists, invertebrates, and fish. The crucial role in stream ecosystems and excellent indicator properties of algae make them an important component of environmental studies to assess the effects of human activities on stream health.

Relations among lotic benthic algal assemblages and various environmental factors associated with water pollution and landscape alteration have been studied intensively (Stevenson et al. 1996), but only a few studies have focused specifically on the effects of urbanization. Algal vegetation in running waters has been studied in many urban areas, including temperate zones (e.g., Whitton 1984; Sabater et al. 1987; Lobo et al. 1995; Vis et al. 1998; Winter and Duthie 1998; Fukushima 1999; Siva et al. 2001; Sonneman et al. 2001) and tropics (Nather Khan 1991; Wu 1999). Studies in individual urban streams or individual metropolitan areas generally have been carried out to determine which attributes of algal assemblages are indicative of human influences for use in future monitoring programs. Many of these described changes in taxonomic composition of assemblages in flowing waters influenced by municipal or industrial wastes when compared to less affected sites. Some also reported declining diversity of algae in severely polluted urban rivers (Whitton 1984; Nather Khan 1991) and increased algal biomass (Taylor et al. 2004). It is not clear, however, whether stream algal assemblages are affected by urbanization in a similar way in different geographic areas. If they are, then it should be possible to identify the attributes of assemblages that can be used as universal indicators of the effects of urbanization. Urban areas differ, however, in their environmental settings and history of development. Climate, geology, and human influences are considered to be ultimate environmental factors that determine biomass and composition of algal assemblages in streams (Biggs 1990; Stevenson 1997). These factors may modify the patterns of algal assemblage variations along urbanization gradients. To understand to what degree the responses of stream algal assemblages to urbanization vary geographically, it is necessary to conduct studies based on a common approach and methodology in various urban areas.

We studied stream algal assemblages in three metropolitan areas of contrasting climate and geography. This investigation was part of the Urban Land Use Gradient (ULUG) study conducted in 2000 as part of the U.S. Geological Survey's (USGS) National Water-Quality Assessment (NAWQA) Program (Tate et al. 2005; this volume). Our goals were to (1) describe relations between urbanization and attributes of stream algal assemblages, such as biomass, diversity, and species composition; and (2) determine whether patterns of algal assemblages along urbanization gradients were different in three metropolitan areas. Uniform responses of particular attributes of algal assemblages to urbanization indicate the possibility of using these attributes as universal bioassessment tools in urban streams. Conversely, large differences among patterns of algal assemblages in three metropolitan areas indicate the overriding influence of local environmental and historical conditions and the need to develop region-specific bioassessment tools.

Methods

Site Selection

The study was conducted in three diverse metropolitan areas in terms of climate and geography—Boston (BOS), Massachusetts, representing the cool and humid Northeast; Birmingham (BIR), Alabama, representing the warm and humid Southeast; and Salt Lake City (SLC), Utah, representing the arid West. In each area, 30 stream sites were selected along gradients of urban intensity quantified by using the multimetric urban intensity index (UII). The UII combined several land-cover, population, socioeconomic, and infrastructure variables (McMahon and Cuffney 2000). In each study area, a group of candidate basins was established to represent a gradient from low (background) to high urban intensity within a relatively homogeneous environmental setting, and several variables characterizing human influences and natural variability were calculated for these basins by using geographic information system (GIS) programs. Variables selected to derive the UII were different among the three study areas; in each case, however, they correlated with population density and did not correlate with basin area. The variables were combined to calculate UII values using formulas from McMahon and Cuffney (2000). The calculated values then were adjusted to range from 0 to 100. The final set of 30 sites was selected in each study area with the goal of minimizing variability in soils, geology, ecoregion, physiographic province, climate, drainage area, and topography, which influence the physical, chemical, and biological characteristics of streams. Finally, the UII was recalculated so the values ranged from 0 to 100 in each set of 30 sites. Greater details of the process of index development, site selection, and lists of variables used to derive the UII in each study area are provided in Tate et al. (2005).

All 30 sites in the BOS study are within or adjacent to ecological subsection 221Ai, Gulf of Maine Coastal Plain, of the U.S. Forest Service ecological unit 221A, Southern New England Coastal Hills and Plain (Keys et al. 1995), which corresponds to the U.S. Environmental Protection Agency (USEPA) level III ecoregion, Northeastern Coastal Zone (Omernik 1995). The BIR study sites are within the USEPA level IV ecoregion, Southern Limestone/Dolomite Valleys and Low Rolling Hills. The final number of sampling sites in BIR area was 27 because of logistical problems. Streams sampled in the SLC originate in the Wasatch Mountain range in the USEPA level III ecoregion, Wasatch and Uinta Mountains, but the urban areas mostly are in lower parts of stream drainage basins in the Central Basin and Range ecoregion. Only 13 perennial streams were available for study in this area because of the dry climate and numerous water diversions. One to three sites were selected in each of the stream basins in the SLC study area for a total number of 30 sites.

Sample Collection and Laboratory Analyses

Benthic algae were sampled as described by Porter et al. (1993). At each site, two quantitative samples were collected—one from hard substrates, mostly rocks located in a riffle or run (richest-targeted habitat or RTH sample), and the other from soft sediment in a depositional area (depositional-targeted habitat or DTH sample). Richest-targeted habitat samples were collected by scraping algae from cobble-size stones selected from five riffle areas of the sampling reach. The scraped area was determined by the foil-template method. Depositional-targeted habitat samples were collected from five depositional areas in the same sampling reach by pressing an inverted petri dish into the sediment and sliding a spatula under the petri dish to isolate the upper layer of sediment. Additionally, a multihabitat qualitative sample (QMH) was collected from various substrates in the sampling reach. Subsamples of RTH samples were taken for determinations of chlorophyll *a*. The other samples and remaining portion of RTH samples were preserved with a 5% solution of formalin for identification and enumeration of algae. Algal samples were collected in low-flow conditions from August 1 to September 1, 2000, in the BOS study area; from June 6 to June 12, 2000, in the BIR study area, and from July 17 to August 9, 2000, in the SLC study area.

Algae were identified and enumerated following protocols in Charles et al. (2002) by taxonomic specialists in the Phycology Section of the Patrick Center for Environmental Research, Academy of Natural Sciences, Philadelphia, and in the Department of Zoology at Michigan State University. Algae were identified and enumerated using the Palmer-Maloney counting cell. Diatoms were identified from permanent slides; only the total number of live and dead diatoms was recorded using the Palmer-Maloney counting cell. Cell density was expressed as number of cells/cm^2 and cell biovolume as mm^3/cm^2. Chlorophyll *a* (mg/m^2) was measured at the USGS Water Quality Laboratory in Lakewood, Colorado, using standard methods (Arar and Collins 1997).

Invertebrates and fish were sampled concurrently with algae. The data used in this study include absolute abundance of invertebrate scrapers in all three study areas and abundance of herbivorous fish in the BIR study area. Herbivorous fish were absent in the BOS and SLC study areas.

Water quality samples were collected in August 2000 in the BOS area, in May 2000 in the BIR area, and in July 2000 in the SLC area. Dissolved oxygen, alkalinity, pH, and conductivity were measured in the field according to Shelton (1994). Nutrient concentrations, major ions, and pesticides were analyzed at the USGS Water Quality Laboratory in Lakewood, Colorado, following methods described in Fishman (1993). Water quality characteristics that were used as explanatory environmental variables for this investigation are listed in Table 1.

Physical habitat characteristics were measured according to Fitzpatrick et al. (1998) close to the time of algal sampling. Physical habitat characteristics were measured at 11 equally spaced transects along the sampling reaches and consisted of measurements of current velocity, discharge, channel morphology, bed substrate, and canopy cover. Means and coefficients of variation (CV) were calculated from these data to characterize general habitat conditions of the reaches. Channel shape index was calculated as $W/D^{D/D\max}$,

TABLE 1. Environmental characteristics used as explanatory variables in the analyses of algal data. Physical habitat variables were derived from measurements made at 11 transects at each sampling site. Abbreviations are given for some variables shown in tables and graphs.

Variable group and description	Abbreviation
Basin-scale characteristics	
Urban intensity index	UII
Basin area (km^2)	
1999 population density (people/km^2)	Population
Road density (km/km^2)	
Number of dams (number/100km^2)	
Land use/land cover (% of basin area)	
Water and wetlands	
Urban	
Barren	
Forest	
Shrub land	
Herbaceous upland/grassland	Grassland
Herbaceous planted/cultivated	Cultivated
Wetlands	
Elevation (m)	
Sampling site	
Mean in basin	
Range in basin	Relief
Percentage of the basin area with slope less than 1%	
Percentage of the basin area with slope less than 1% at elevations above average	Uplands
Percentage of the basin area with slope less than 1% at elevations below average	
Stream order	
Physical habitat characteristics	
Segment sinuosity	
Reach sinuosity	
Surface-water gradient (m/km)	Gradient
Percentage of reach area as pools	
Percentage of reach area as riffles	
Percentage of reach area as runs	
Wetted width (m)	
Coefficient of variation of wetted width	
Maximum wetted width (m)	
Bank-full width (m)	
Coefficient of variation of bank-full width	
Maximum bank-full width (m)	
Wetted depth (m)	
Coefficient of variation of wetted depth	
Maximum wetted depth (m)	
Bank-full depth (m)	
Coefficient of variation of bank-full depth	
Maximum bank-full depth (m)	
Depth at the sampling location (m)	
Wetted width–depth ratio	
Coefficient of variation of wetted width–depth ratio	
Bank-full width–depth ratio	
Coefficient of variation of bank-full width–depth ratio	
Channel shape index	
Coefficient of variation of channel shape index	

TABLE 1. Continued.

Variable group and description	Abbreviation
Discharge (m^3/s)	
Coefficient of variation of discharge	
Mean flow velocity (m/s)	
Coefficient of variation of flow velocity	
Maximum flow velocity (m/s)	
Flow velocity at the sampling location (m/s)	
Shear stress	
Froude number	
Stream power (W/m)	
Flow-stability index	
Mean dominant substrate size	
Coefficient of variation of dominant substrate size	
Silt occurrence	
Percentage of nonporous substrate	
Percentage of fine sediments	% fine
Percentage of silt-clay size particles	% silt + clay
Percentage of sand size particles	% sand
Percentage of gravel size particles	% gravel
Percentage of cobble size particles	% gravel
Percentage of boulder size particles	
Percentage of silt-gravel size particles	% silt + gravel
Percentage of gravel-cobble size particles	
Percentage of cobble-boulder size particles	
Embeddedness (%)	
Manning's channel roughness	
Channel relative roughness	
Hydrological channel radius	
Canopy closure (%)	
Coefficient of variation of canopy closure	
Light intensity (photosynthetically active radiation, mmol s^{-1} m^{-2})	Light
Hydrological (stage-related) characteristics	
Variation of stage values	
Skew of stage values	
Number of time periods when stage rises by at least 0.03 m/h	periodr1
Number of time periods when stage rises by at least 0.09 m/h	periodr3
Number of time periods when stage rises by at least 0.15 m/h	periodr5
Number of time periods when stage rises by at least 0.21 m/h	periodr7
Number of time periods when stage rises by at least 0.27 m/h	periodr9
Number of time periods when stage falls by at least 0.03 m/h	periodf1
Number of time periods when stage falls by at least 0.09 m/h	periodf3
Number of time periods when stage falls by at least 0.15 m/h	periodf5
Number of time periods when stage falls by at least 0.21 m/h	periodf7
Number of time periods when stage falls by at least 0.27 m/h	periodf9
Maximum duration of low stage pulses with discharge < 5th percentile as low flow (h)	Mxl5
Maximum duration of low stage pulses with discharge < 10th percentile as low flow (h)	Mxl10
Maximum duration of low stage pulses with discharge < 25th percentile as low flow (h)	Mxl25
Median duration of low stage pulses with discharge < 5th percentile as low flow (h)	Mdl5
Median duration of low stage pulses with discharge < 10th percentile as low flow (h)	Mdl10
Median duration of low stage pulses with discharge < 25th percentile as low flow (h)	Mdl25

TABLE 1. Continued.

Variable group and description	Abbreviation
Maximum duration of high stage pulses with discharge > 75th percentile as high flow (h)	Mxh75
Maximum duration of high stage pulses with discharge > 90th percentile as high flow (h)	Mxh90
Maximum duration of high stage pulses with discharge > 95th percentile as high flow (h)	Mxh95
Median duration of high stage pulses with discharge > 75th percentile as high flow (h)	Mdh75
Median duration of high stage pulses with discharge > 90th percentile as high flow (h)	Mdh90
Median duration of high stage pulses with discharge > 95th percentile as high flow (h)	Mdh95
Water chemical and physical characteristics	
Phosphorus as total phosphorus (mg/L as P)	TP
Phosphorus as orthophosphate, dissolved (mg/L as P)	PO_4
Nitrogen as total nitrogen (mg/L as N)	TN
Nitrogen as total organic nitrogen + dissolved ammonia (mg/L as N)	TKN
Nitrogen as nitrite + nitrate nitrogen, dissolved (mg/L as N)	$NO_2 + NO_3$
Nitrogen as ammonia, dissolved (mg/L as N)	NH_4
Conductivity (mS/cm)	Cond
Alkalinity (mg/L as $CaCO_3$)	
pH (standard units)	
Sulfate, dissolved (mg/L)	SO_4
Chloride, dissolved (mg/L)	Cl
Calcium, dissolved (mg/L)	Ca
Magnesium, dissolved (mg/L)	Mg
Sodium, dissolved (mg/L)	Na
Potassium, dissolved (mg/L)	K
Fluoride, dissolved (mg/L)	F
Iron, dissolved (mg/L)	Fe
Silica as silica dioxide, dissolved (mg/L)	SiO_2
Residue on evaporation at 180°C (mg/L)	
Total herbicide concentration (mg/L)	HerbConc
Number of herbicide detections per sample	HerbHits
Total pesticide concentration (mg/L)	
Number of pesticide detections	
Oxygen, dissolved (mg/L)	O_2
Water temperature (°C)	
Turbidity (NTU)	
Grazers	
Abundance of invertebrate scrapers (number/m^2)	Scrapers
Abundance of herbivorous fish largescale stoneroller (in BIR, number/reach)	Stoneroller

where W is wetted channel width, *D* is mean water depth, and Dmax is maximum water depth. Smaller values of the shape index generally indicate more pool-like conditions, whereas larger values indicate more riffle-like conditions. The flow-stability index characterized high-flow events and was calculated as D_{lf}/D_{bf}, where D_{lf} is depth of water at low flow, and D_{bf} is bank-full depth. Current velocity, water depth, and light intensity also were measured at the sampling location (except light intensity in the BIR study area). Mean light intensity (photosynthetically active radiation, PAR) measured near the stream bottom with light meters was used in the analyses. More detailed information on the physical habitat characterization can be found in Short et al. (2005, this volume) and in Fitzpatrick et al. (1998).

Stream stage (water level) was recorded at 15-min intervals at each site using USGS gauges or stage transducers (McMahon et al. 2003). Summary hydrological variables were calculated from the recorded stage data and used in our analyses as measures of flow stability. Watershed-scale land-use, population, infrastructure, and socioeconomic variables in each watershed were derived from GIS data. All environmental variables used in this study are listed in Table 1.

Data Analysis

Algal biomass was characterized by the amount of chlorophyll *a* in RTH samples and the total algal biovolume in RTH and DTH samples. Relations between algal biomass and environmental variables were evaluated by using correlation analysis (Pearson's *r*). The number of environmental variables in our data set was higher (>100) than the number of observations in each of the regional data sets (27–30). Thus, some correlations may be spurious, caused by chance alone. To avoid overinterpretation, we sought combinations of a few variables that could explain biomass variability. This was accomplished by stepwise forward selection of variables in multivariate regression analysis. Initially, we selected 10–12 variables representing different classes, such as nutrients (TP and TN), major ion chemistry (conductivity and alkalinity), pH, light, sediment size, channel morphology, flow variability, and abundance of grazers. These variables were chosen so that they were not highly intercorrelated with each other but had significant correlation with algal biomass. The criteria for variable inclusion in the model was $F > 0.05$, and for exclusion, $F < 0.1$. Resulting models had one to three variables that explained observed biomass variability in the most parsimonious way. The low number of variables is reasonable for small data sets such as ours. Total algal biovolume and concentration of nutrients, ions, alkalinity, and conductivity were log-transformed prior to analyses. Correlation and multiple regression procedures were conducted using SPSS for Windows, version 11.0.

Algal diversity was estimated by species richness, which is the total number of species in a sample, and Shannon-Wiener diversity index, which is a function of both species richness and evenness of species distribution. Both metrics are commonly used in water quality bioassessment (Stevenson and Bahls 1999). We also calculated relative abundance of algal taxa that are currently considered as possibly endemic. Trends in algal diversity along urban gradient were evaluated by calculating Kendall's correlations between these diversity measures and UII.

To evaluate patterns in taxonomic composition of algal assemblages and their relations with stream environment, we used nonmetric multidimensional scaling (NMS, Kruskal 1964; Mather 1976). Nonmetric multidimensional scaling is a nonparametric iterative technique using ranked distances, and this technique is used increasingly in ecological studies (McCune and Mefford 1999). Nonmetric multidimensional scaling solution is based on minimizing stress, which is a measure of poorness of fit between the ordination matrix and original data matrix. To run NMS, we used the "slow-and-thorough" autopilot mode available in PC-ORD 4.0 (McCune and Mefford 1999) and the quantitative Sørensen (Bray-Curtis) distance measure. Three-dimensional solutions were optimal in all NMS runs. Four algal data sets from each study area were used, representing samples from two habitats (RTH and DTH) and including either diatom proportions or all algal taxa proportions. Species relative abundance was square root transformed. We rotated ordinations to load the variable UII on a single (horizontal) axis and illustrated relations between algal assemblages and environment with the joint plots. These plots showed the positions of taxa and selected environmental variables most strongly correlated with ordination axes and related to different aspects of stream environment (e.g., hydrology, substrate composition, light regime, ionic composition, nutrients). Variance explained by ordination was expressed by the coefficient of determination (r^2) between Euclidean distances in the ordination space and Sørensen distances in the original species spaces. Algal taxa shown in the ordination plots are those that had the highest correlations with ordination axes and were found in at least three samples in each data set. The relative importance of environmental variables in explaining assemblage composition patterns was estimated by the sum of squared correlations between a variable and all ordination axes (Σr^2).

Kendall's correlations between relative abundance of most abundant (reaching 15% or 20%) algal taxa and UII were calculated to identify which taxa were associated with urban gradient in each study area. Autecological characteristics of algal taxa, such as trophic categories, relations to water mineral content and pollution tolerance, were obtained from the works of Sládecek (1973), Lange-Bertalot (1979), and van Dam et al. (1994). These sources are useful for characterizing the autecology of cosmopolitan taxa; however, metrics calculated from these characteristics, such as percentage of pollution-sensitive, pollution-tolerant, oligo- and polysaprobic (tolerance to organic pollution), and oligo- and eutraphentic (tolerance to nutrient enrichment) taxa, must be considered with caution. These sources provide no autecological information for many algal taxa found in American streams.

Results

Habitat Characteristics

The three study areas differed in climate, topography, and geology, and therefore, in water chemistry and flow regime (Table 2). Water-mineral content, as measured by conductivity, was generally higher in the SLC area than in the other two study areas because of the arid climate. In the BIR area, conductivity and pH were relatively high because of the prevalence of carbonate bedrock. In the BOS area, conductivity and pH were lowest among three areas because of the prevalence of noncarbonate bedrock and the cool, humid climate. Conductivity was significantly positively correlated with the UII in all three study areas (Table 2). Water pH tended to be higher in urbanized streams in all three study areas, but we found no significant correlation between pH and the UII (Table 2).

Streams in the SLC area had the steepest channels, whereas streams in the BIR area had the lowest gradients and flow velocities. Flow stability, as quantified by the flow-stability index derived from channel morphology, increased with urbanization in the BOS study area, and showed no pattern in the BIR and SLC areas (Table 2).

Streams in the BIR area had, in general, a higher proportion of sand in the bed sediment than streams in the BOS and SLC areas (Table 2). In BOS and SLC, proportions of sand were low in the nonurban streams but increased along gradients of urbanization. Some of the high-gradient nonurban stream sites in the SLC area had very rough channels with numerous boulders.

The dominant natural land-cover type in the two eastern study areas was forest; in the SLC study area, the dominant natural land-cover type was shrub land (Table 2). Cultivated land cover was present in all three study areas, but it was significantly negatively correlated with the UII only in the BIR area. In correspondence with this pattern, nutrient concentrations increased with urbanization in the BOS and SLC areas, but not in the BIR area. Median nutrient concentrations were comparable in all study areas. One site with exceptionally high phosphorus and ionic (NaCl) content was in the BIR area. Concentrations of herbicides were higher in urbanized streams than in less urbanized streams, but significant positive correlations between herbicide concentrations and UII were found only in the BIR and SLC areas.

Biomass of Benthic Algae in Streams

Regional differences.—Median algal biovolume was highest in the BIR study area and lowest in the BOS study area (Figure 1A). Total algal biovolume was consistently higher in DTH samples than in RTH samples in all three areas, although the difference in biovolume between DTH and RTH samples was not large in the SLC area. In the BOS and BIR study areas, algal biovolume was approximately one order of magnitude higher in DTH samples than in RTH samples. Median chlorophyll *a* was lowest in the BOS area and highest in the SLC area (Figure 1B). A chlorophyll-*a* concentration of 200 mg/m^2, commonly considered a nuisance level (Biggs 1996; Dodds et al. 1998), occurred in only two BIR streams of relatively low urban intensity (UII = 16.5–16.8) and in five SLC streams of moderate to high urban intensity (UII = 45.5–71.3). Values between 50 and 200 mg/m^2, which also can be regarded as a nuisance level (Biggs 1996), were observed at nine sites of varying degrees of urbanization in the SLC area, at seven sites in the BIR area, and at three sites of rather high urban intensity (UII = 62.7–92.6) in the BOS area.

Boston study area.—In the BOS area, algal biomass increased along the urban intensity gradient. Positive correlation between the UII and total algal biovolume was significant for RTH samples ($r = 0.53$, $P < 0.01$) but not significant for DTH samples ($r = 0.12$). Chlorophyll *a* concentration in RTH samples also was significantly positively correlated with the UII ($r = 0.48$, $P < 0.01$). Diatoms were the most abundant algae in DTH samples and the second most abundant algae in RTH samples (Figure 2A, B). Red algae constituted most of the algal biomass in RTH samples (Figure 2A).

In the BOS study area, total algal biovolume in RTH samples was significantly positively correlated with nutrients (all measured forms of phosphorus and nitrogen, $r = 0.36$–0.50, $P < 0.05$), alkalinity ($r = 0.45$, $P < 0.05$), conductivity ($r = 0.52$, $P < 0.01$), water depth ($r = 0.47$, $P < 0.05$), flow-stability index ($r = 0.57$, $P < 0.01$), proportion of fine sediments ($r = 0.53$, $P < 0.01$), number of dams ($r = 0.44$, $P < 0.05$), and light intensity ($r = 0.44$, $P < 0.05$). Total algal biovolume was significantly negatively correlated with channel width ($r = -0.36$, $P < 0.05$). The significance of these correlations, however, must be regarded with caution. The high number of tested variables increased the possibility of a spurious correlation.

TABLE 2. Selected characteristics of streams in three study areas and correlations of these characteristics (Kendall's correlation coefficient, tau) with the urban intensity index. Abbreviations for variables are in Table 1. Median values are in bold. **, $P < 0.01$; *, $P < 0.05$.

	Boston				Birmingham				Salt Lake City			
Characteristics	Min	Median	Max	Tau	Min	Median	Max	Tau	Min	Median	Max	Tau
Urban (%)	1	**15**	67	0.87**	0	**13**	73	0.93**	0	**40**	87	0.81**
Forest (%)	23	**65**	86	–0.89**	18	**64**	93	–0.74**	2	**11**	47	–0.49**
Shrub land (%)	0	**0**	0		0	**0**	0		1	**12**	68	–0.68**
Grassland (%)	2	**7**	17	–0.28*	0	**0**	0		0	**4**	26	–0.52**
Cultivated (%)	3	**8**	16	0.01	3	**13**	34	–0.31*	0	**16**	53	0.09
Number of dams	0	**5**	17	0.45**								
Surface-water gradient (m/km)	1.2	**5.8**	16.2	–0.16	0.3	**3.9**	6.7	0.03	4.0	**10.1**	166.1	–0.12
Wetted width (m)	5.0	**9.3**	12.5	–0.13	3.9	**5.6**	15.1	0.08	1.2	**4.4**	13.5	–0.05
Wetted depth (m)	0.16	**0.30**	0.62	0.57**	0.05	**0.25**	0.44	–0.14	0.05	**0.21**	0.56	–0.02
Discharge (m^3/s)	0.18	**0.68**	2.85	0.32*	0.001	**0.27**	4.19	0.04	0.001	**0.24**	3.87	–0.10
Mean flow velocity (m/s)	0.12	**0.31**	0.50	0.33*	0.001	**0.07**	0.56	0.01	0.03	**0.29**	0.67	–0.20
Flow-stability index	0.24	**0.37**	0.51	0.32*	0.10	**0.19**	0.47	–0.23	0.10	**0.32**	0.78	–0.01
% silt + clay	0	**0**	15	0.19	0	**0**	27	–0.27	0	**0**	21	0.25
% sand	0	**2**	45	0.42**	0	**13**	79	–0.03	0	**3**	88	0.31*
% cobbles	18	**67**	100	–0.28	0	**19**	70	–0.17	0	**38**	91	–0.01
% boulders	0	**12**	52	0.09	0	**9**	64	0.26	0	**17**	76	–0.21
Embeddedness (%)	16	**34**	86	0.30*	9	**66**	100	0.31*	26	**61**	100	0.02
Channel relative roughness	11	**33**	68	–0.53**	18	**35**	141	0.07	7	**37**	204	–0.07
Conductivity (mS/cm)	47	**224**	643	0.69**	168	**314**	1,710	0.42**	89	**540**	1,110	0.37**
pH	6.4	**6.9**	7.6	0.26	7.5	**8.0**	8.3	0.14	7.3	**8.1**	8.6	0.13
TP (mg/L as P)	0.01	**0.03**	0.25	0.34*	0.01	**0.02**	8.93	0.08	0.01	**0.04**	0.13	0.35**
TN (mg/L as N)	0.32	**0.60**	5.40	0.45*	0.22	**0.78**	3.54	0.21	0.17	**0.75**	3.51	0.15
Total herbicide concentration (mg/L)	0.000	**0.003**	0.324	0.27	0.022	**0.030**	0.060	0.44**	0.001	**0.027**	1.372	0.49**
Number of herbicide detections	0	**1**	4	0.20	0	**3**	7	0.53**	1	**3**	7	0.42**
Light (mmol s^{-1} m^{-2})	0.4	**7.5**	101	0.15					2.1	**23.2**	670.4	–0.26
Number of herbivorous fish					2	**73**	706	0.61**				

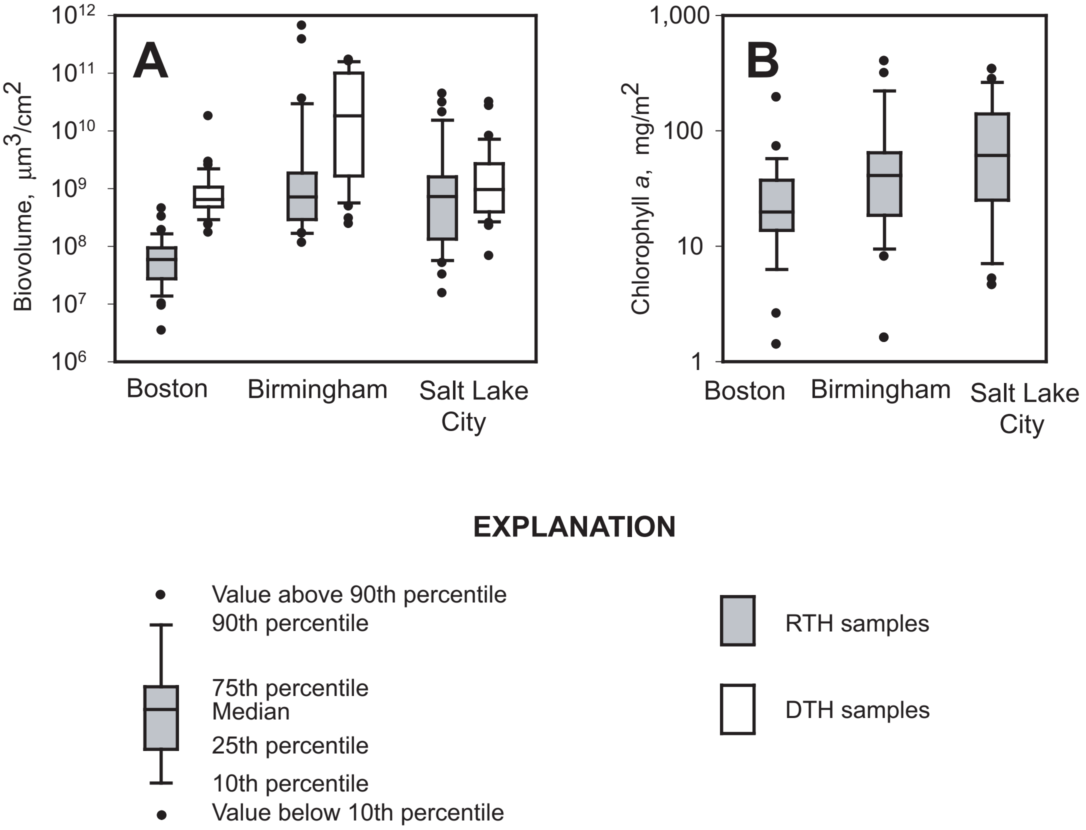

FIGURE 1. Box plots of the (A) total algal biovolume and (B) chlorophyll *a* in streams in three study areas—Boston n = 30; Birmingham n = 27; and Salt Lake City n = 30 for RTH samples, n = 28 for DTH samples.

For the stepwise multiple regression analysis, the following variables were selected initially as possible independent variables: TP, TN, alkalinity, wetted channel width, flow-stability index, percentage of fine sediments, current velocity and depth at the sampling location, light, and abundance of invertebrate scrapers. Variables finally chosen by the stepwise forward-selection procedure as those best predicting total algal biovolume on rocks were flow stability and TN (Table 3). Final variables in the chlorophyll-*a* model were light and TP (Table 3). Total algal biovolume in DTH samples could not be predicted from measured environmental factors. Although the relatively low number of observations in our data sets did not allow us to create highly predictive models, results of the selection of variables indicated that the main factors associated with increased algal biomass on rocks in urban streams of the BOS area were nutrients, light, and flow stability.

Birmingham study area.—In the BIR study area, algal biovolume was lower in streams at the high end of the urban gradient (Figure 2C, D). Negative correlation between the UII and total algal biovolume was significant for DTH samples ($r = -0.53$, $P < 0.01$) but not significant for RTH samples ($r = -0.33$). No trend was detected in chlorophyll *a* along the urban gradient. Correlation analysis showed that algal biovolume was positively correlated ($P < 0.05$) with a number of variables that had decreasing values along the urban gradient, including segment sinuosity ($r = 0.43$, $P < 0.05$ in RTH samples and $r = 0.44$, $P < 0.05$ in DTH samples), turbidity ($r = 0.42$, $P < 0.05$ in RTH samples and $r = 0.39$, $P < 0.05$ in DTH samples), concentration of suspended solids ($r = 0.42$, $P < 0.05$ in both RTH and DTH samples), percentage of gravel in the sediment ($r = 0.40$, $P < 0.05$ in RTH samples), and variation in discharge ($r = 0.46$, $P < 0.05$ in RTH samples), and was negatively correlated with variables that had increasing values along the urban gradient, such as surface water gradient ($r = -0.41$, $P < 0.05$ in DTH samples) and channel width ($r = -0.42$, $P < 0.05$ in RTH samples

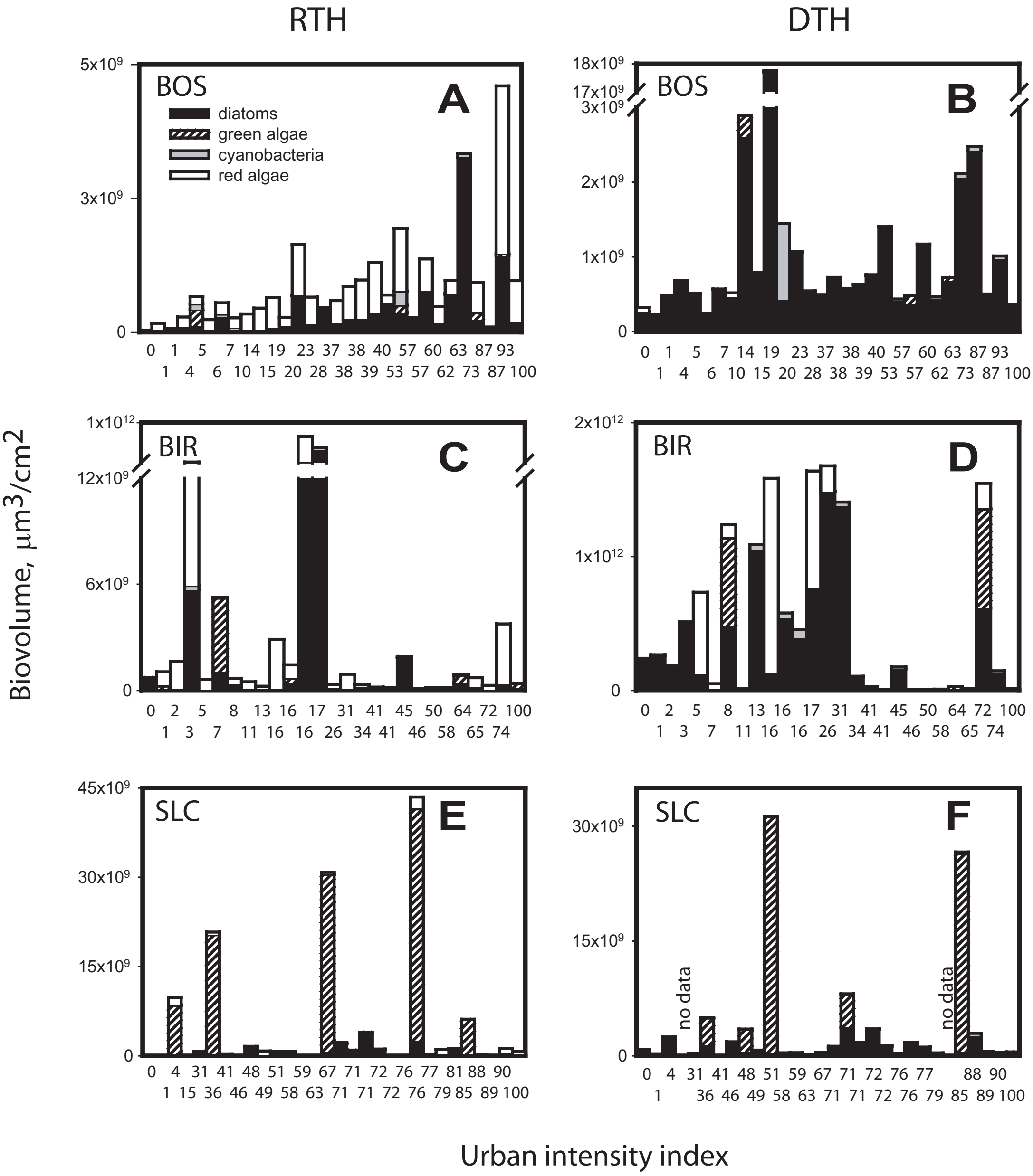

FIGURE 2. Algal biovolume in streams in (A, B) Boston (BOS); (C, D) Birmingham (BIR); and (E, F) Salt Lake City (SLC); A, C, E—hard substrata (RTH samples); B, D, F—soft sediments (DTH samples). The order of the sampling sites is by increasing UII.

and $r = -0.51$, $P < 0.01$ in DTH samples). The strongest correlations occurred between algal biovolume and abundance of the herbivorous fish, the largescale stoneroller *Campostoma oligolepis* ($r = -0.50$, $P < 0.01$ in RTH samples and $r = -0.77$, $P < 0.01$ in DTH samples). Stepwise forward selection of variables in multiple regression analysis confirmed that abundance of largescale stoneroller most likely explained the decrease in algal biovolume in the BIR streams (Table 3). Potential explanatory variables tested in the multiple regression model were TP, TN, alkalinity, channel width, flow stability, canopy closure, turbidity, percentage of

TABLE 3. Results of the stepwise multiple regression analysis with three algal biomass characteristics (biovolume of algae in RTH and DTH samples, and chlorophyll *a*) as dependent variables. Explanatory variables were selected by the stepwise forward procedure as best predictors of algal biomass. No environmental variables were selected as predictors in two data sets—algal biovolume of DTH samples in the BOS study area and chlorophyll *a* in the BIR study area.

Dependent variable	Model r^2	Adjusted model r^2	Explanatory variables	Beta	r^2
		Boston			
Total algal biovolume, RTH	0.44	0.40	Flow-stability index	0.47	0.33
			Log TN	0.35	0.11
Chlorophyll *a*	0.72	0.70	Light	0.69	0.62
			Log TP	0.33	0.10
		Birmingham			
Total algal biovolume, RTH	0.25	0.22	Stoneroller abundance	–0.51	0.25
Total algal biovolume, DTH	0.67	0.56	Stoneroller abundance	–0.77	0.58
			Alkalinity	0.31	0.09
		Salt Lake City			
Total algal biovolume, RTH	0.16	0.13	Stream width		0.16
Total algal biovolume, DTH	0.42	0.37	Stream width	1.12	0.29
			Stream depth	–0.68	0.13
Chlorophyll *a*	0.19	0.16	Basin area with slope < 1%	0.43	0.19

fine-grained sediments, abundance of largescale stoneroller, stream depth, and current velocity at the sampling site. The final model for algal biovolume in RTH samples included only largescale stoneroller abundance as an explanatory variable, and the model for DTH samples includes abundance of largescale stoneroller and alkalinity. Diatoms and red algae most often dominated algal assemblages in this area, showing no particular pattern of relative abundance along the urban gradient (Figure 2C, D).

Salt Lake City study area.—No pattern was observed in algal biomass along the urban gradient in streams of the SLC study area. The filamentous green alga *Cladophora glomerata* occasionally proliferated in streams with various degrees of urban intensity (Figure 2E, F). Weak positive correlations ($r = 0.37$–0.53, $P < 0.05$) were identified between algal biomass variables (total algal biovolume and chlorophyll *a)* and several variables representing stream width and flatness of the watershed estimated as percentage of watershed area with slopes less than 1%. Biovolume in RTH samples was negatively associated with hydrologic variables related to flow stability, but the number of sites with hydrologic data were too low to ascertain the significance of these correlations. Stepwise multiple regression analysis did not reveal any relations between algal biomass and environmental factors except for a tendency toward higher biomass in wider streams and streams with flatter watersheds (Table 3). Variables initially considered for inclusion in the models were TP, TN, alkalinity, light, percentage of fine-grained sediment, stream width, stream depth, and current velocity at the sampling site, flow-stability index, percentage of the watershed with slope less than 1%, and abundance of invertebrate scrapers. Only stream depth, width, and percentage of the watershed with slope less than 1% were selected by the stepwise procedure for the final equations (Table 3).

Algal Diversity

The diversity of stream algal assemblages differed among the three study areas (Figure 3). The total number of species in a sample (species richness) was higher in the BIR study area compared with the other two areas (Figure 3A). Total number of algal species (gamma diversity) reported for the BIR data set also was higher (358 taxa) than for the BOS (278 taxa) and SLC (291 taxa) data sets. The Shannon-Wiener diversity index, however, was similar in all study areas. This index was somewhat higher in soft-sediment samples in the BOS area (Figure 3B), which can be explained by the absence of filamentous green algae. Evenness usually is low when there is an abundant growth of filamentous algae and high when filamentous algae are absent.

The strongest positive correlation between diversity of algal assemblages and urban gradient occurred in streams of the BOS study area (Tables 4, 5). In the SLC area, algal assemblages in DTH and QMH

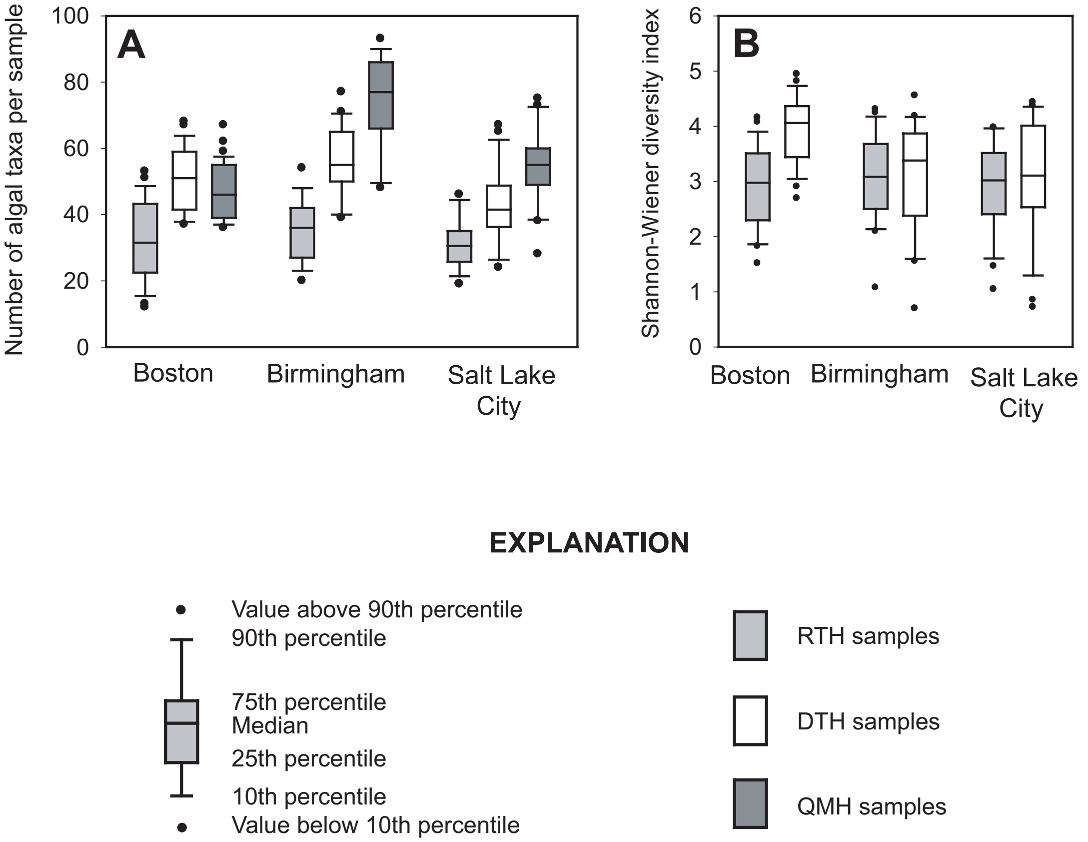

FIGURE 3. Median values and ranges of (A) total species richness and (B) Shannon-Wiener diversity index in streams of three study areas: Boston *n* = 30; Birmingham *n* = 27 for RTH and DTH samples and *n* = 17 for QMH samples; and Salt Lake City *n* = 30 for RTH samples, *n* = 28 for DTH samples, and *n* = 27 for QMH samples.

samples also had higher diversity in urban rivers. In the BIR area, only species richness in DTH samples was lower in urban streams than in nonurban streams.

Taxa with the highest number of occurrences in all study areas generally were cosmopolitan diatoms, such as *Achnanthidium minutissimum*, *Cocconeis placentula* var. *lineata*, *Navicula cryptotenella,* and *Gomphonema parvulum,* which are common in temperate rivers. There were, however, obvious regional differences in the taxonomic composition of algal assemblages. In the BOS study area, the list of taxa with the highest occurrences included a number of oligohalobous (salt intolerant) taxa, such as *Tabellaria flocculosa, Achnanthidium rivulare*, and *Eunotia incisa*. Conversely, in the BIR and SLC study areas, diatoms known to prefer high water-mineral content were common, including *Rhoicosphenia abbreviata, Achnanthidium deflexum, Nitzschia paleacea,* and *N. dissipata.* Besides these widely distributed taxa, some species with limited geographic distribution were found. The

TABLE 4. Kendall rank correlation between the Shannon-Wiener diversity index of algal assemblages and the urban intensity index in the three study areas. **, $P < 0.01$, *, $P < 0.05$.

	All algal taxa		Diatoms only	
Study area	RTH	DTH	RTH	DTH
Boston (*n* = 30)	0.59**	0.26*	0.63**	0.30*
Birmingham (*n* = 27)	–0.05	–0.09	0.03	–0.24
Salt Lake City (*n* = 30 for RTH; *n* = 28 for DTH)	0.24	0.05	0.24	0.42**

TABLE 5. Kendall rank correlation coefficients between species richness of algal assemblages and the urban intensity index in the three study areas. **, $P < 0.01$, *, $P < 0.05$.

	All algal taxa			Diatoms only		
Study area	RTH	DTH	QMH	RTH	DTH	QMH
Boston (n = 30)	0.66**	0.27*	0.30*	0.67**	0.28*	0.30*
Birmingham (n = 27 for RTH and DTH; n = 17 for QMH)	–0.02	–0.29*	–0.31	–0.04	–0.32*	–0.33
Salt Lake City (n = 30 for RTH; n = 28 for DTH; n = 27 for QMH)	0.21	0.47**	0.35*	0.22	0.44**	0.39*

highest number of rare and yet undescribed taxa was found in the BIR area. At least six diatom species, one green alga, and one chrysophyte were undescribed species, currently found only in the southeastern United States. Correlations (Kendall's tau), however, between the UII and relative abundance (RTH and DTH samples) and occurrence (RTH, DTH, and QMH samples) of these possibly endemic taxa in the BIR data set were not significant.

In the SLC study area, one diatom species (*Navicula* sp.) was found that is new to science and possibly endemic in the western United States. Its occurrence and abundance did not correlate with UII. No species of limited distribution were found in the BOS area.

Trends in Taxonomic Composition

Boston study area.—Algal taxa reaching the highest (20% in at least one sample) relative abundance of cells in the RTH samples collected in streams of the BOS study area were the diatoms *Achnanthidium minutissimum, A. rivulare, Cocconeis placentula* var. *lineata, Gomphonema parvulum;* filamentous cyanobacteria *Homoeothrix simplex, Calothrix fusca, Phormidium formosum, P. aeruginosum, Lyngbya hieronymusii, Lyngbya* sp.; and some red algae not identifiable because of the absence of reproductive structures in the summer. Among these taxa, only relative abundances of *Achnanthidium minutissimum* and *Calothrix fusca* were negatively correlated with UII (Kendall's tau, $P < 0.05$); eutraphentic *Gomphonema parvulum* was positively correlated with UII. In the DTH samples, the most abundant species (a relative abundance of 15% at least once) were the diatoms *Achnanthidium minutissimum, A. rivulare, Cocconeis placentula* var. *lineata, Fragilaria capucina* var. *rumpens, Tabellaria flocculosa, Staurosira construens* var. *venter, Psammothidium subatomoides, Sellaphora seminulum, Brachysira microcephala*, and *Melosira varians.* Among these, only *Achnanthidium minutissimum* and oligotraphentic *Psammothidium subatomoides* were negatively correlated (Kendall's tau, $P < 0.05$) with the UII, and no taxa showed significant positive correlations with the UII.

In the BOS study area, NMS ordinations of both data sets (diatoms and all algal taxa) from the RTH samples produced similar results (Table 6). Variance in species data explained by all-taxa ordination was 87%, and variance explained by diatom ordination was 91%. Both ordinations had strong correlations with the UII. The axis aligned with the UII explained 52% of the variation in the all-taxa and 57% in the diatom data set. Variables strongly correlated with the UII-aligned ordination axis included alkalinity, conductivity, road density, TN, wetted channel width-to-depth ratio, shape index, and channel relative roughness (Table 6). Variables that showed strong association with algal assemblage composition in the BOS study area, but not strongly correlated with the UII, were TP, number of herbicide detections, and some variables characterizing flow regime (Table 6; Figure 4A). Eutraphentic and pollution-tolerant diatoms (*Navicula minima*, *N. gregaria, Sellaphora seminulum*) were positioned at the high end of the urban gradient. Some species in the left side of the ordination diagram, corresponding to the low end of the urban gradient, were oligotraphentic taxa (*Brachysira microcephala* and *B. serians*). Abundance of filamentous cyanobacteria, such as *Lyngbya bergei* and *Calothrix fusca*, was lower in urban streams.

Ordination of DTH samples indicated similar environmental gradients explaining variation in algal assemblages as ordination of RTH samples, although taxa that had the highest ordination scores were different between the two ordinations (compare Figure 4A, B). Diatoms positioned at the high end of the urban gradient were mostly eutraphentic, pollution-tolerant, and halophilic species (*Navicula lanceolata, Rhoicosphenia abbreviata, Nitzschia bremensis*). The all-taxa and diatom ordinations extracted 85% and 91% variability in species data, respectively. After rotation, the first axis aligned with UII extracted 28% and 33% of the varia-

TABLE 6. Correlations of environmental variables and NMS ordination axes for the RTH 30-sample data set for the Boston study area. Ordinations were rotated to maximize loadings of the first axis on the urban intensity index. Only environmental variables with highest multiple r^2 (Σr^2) are shown. Significant correlations ($P < 0.05$) are in bold. Abbreviations for variables and variable units are in Table 1.

	All taxa				Diatoms only			
Environmental variable	axis 1	axis 2	axis 3	Σr^2	axis 1	axis 2	axis 3	Σr^2
Alkalinity	**0.72**	–0.20	0.18	0.59	**0.81**	0.02	**0.38**	0.79
Wetted width–depth ratio	**–0.66**	0.08	–0.27	0.52	**–0.72**	0.02	–0.22	0.57
Channel shape index	**–0.62**	0.09	–0.29	0.48	**–0.66**	0.09	–0.23	0.49
Urban intensity index	**0.67**	0.00	0.07	0.45	**0.83**	–0.03	0.17	0.71
Conductivity	**0.63**	–0.13	0.18	0.44	**0.83**	–0.02	**0.42**	0.87
Road density	**0.64**	0.02	0.10	0.42	**0.74**	–0.11	0.11	0.56
Coefficient of variation of bank-full width–depth	**0.49**	–0.33	0.23	0.40	**0.53**	–0.05	0.34	0.40
TN	**0.50**	–0.33	0.18	0.39	**0.74**	–0.06	**0.49**	0.79
Dissolved oxygen	**–0.51**	0.28	–0.20	0.38	**–0.54**	0.11	–0.10	0.31
Channel relative roughness	**–0.58**	0.12	–0.15	0.37	**–0.70**	–0.08	–0.18	0.54
NO_2+NO_3	**0.49**	–0.32	0.15	0.36	**0.71**	0.01	**0.49**	0.74
TKN	**0.50**	–0.25	0.23	0.36	**0.64**	–0.11	0.30	0.51
SO_4	**0.55**	–0.09	–0.23	0.36	**0.62**	**0.44**	0.11	0.59
Mean flow velocity	**0.50**	–0.28	–0.15	0.35	**0.50**	**0.43**	0.29	0.52
Maximum flow velocity	**0.47**	–0.27	–0.21	0.34	**0.51**	**0.41**	0.31	0.52
Mxh90	0.29	0.18	**0.47**	0.34	0.28	–0.18	0.25	0.17
TP	**0.39**	**–0.38**	0.18	0.33	**0.67**	0.00	**0.51**	0.71
Number of herbicide detections	**0.36**	**–0.41**	0.19	0.33	–0.17	–0.03	–0.15	0.05
Population	**0.56**	0.04	0.04	0.32	**0.71**	–0.10	0.03	0.51
Forest	**–0.52**	–0.21	0.01	0.31	**–0.44**	0.08	0.11	0.21
Segment sinuosity	**–0.52**	0.18	–0.02	0.31	**–0.51**	–0.03	–0.15	0.29
Coefficient of variation of bank-full width	**0.40**	–0.21	0.31	0.31	0.19	–0.20	0.22	0.12
Bank-full width–depth ratio	**–0.51**	0.05	–0.19	0.30	**–0.60**	0.07	–0.16	0.39
Mxl5	–0.33	**0.42**	–0.10	0.29	**–0.44**	0.02	**–0.36**	0.32
Water temperature	**0.42**	–0.26	0.20	0.28	**0.47**	0.20	0.18	0.29
Wetted depth	**0.51**	–0.06	0.14	0.28	**0.66**	–0.17	0.01	0.46
Discharge	**0.36**	–0.34	–0.17	0.27	**0.50**	0.16	0.09	0.28
% silt+gravel	**0.47**	–0.07	0.21	0.26	**0.45**	–0.27	–0.13	0.29
Wetted width	**–0.41**	–0.05	–0.29	0.25	–0.29	0.00	–0.25	0.14
% sand	**0.41**	–0.24	0.11	0.24	**0.45**	–0.18	–0.11	0.25
Maximum wetted depth	**0.46**	–0.05	0.10	0.23	**0.63**	–0.18	–0.01	0.42

tion in all-taxa and diatom data sets, respectively. Similar to the RTH ordination, the variation of algal assemblage along urban gradient was mostly associated with water-mineral content, nitrogen content, and channel morphology (Table 7). Variation in assemblages not directly related to urban intensity gradient was mostly associated with several characteristics of flow regime in both diatom and all-taxa ordinations, with silt occurrence in the all-taxa ordination, and with percentage of riffles in the diatom ordination.

Birmingham study area.—In the BIR study area, the most abundant taxa in both RTH and DTH samples were diatoms *Achnanthidium minutissimum* and *A. deflexum*; filamentous cyanobacteria *Homoeothrix simplex, Phormidium autumnale,* and unidentified *Leptolyngbia*; green alga *Scenedesmus acutus*; and the chantransia stage of red algae. Among these, only relative abundance of *Scenedesmus acutus* increased significantly with urbanization.

Ordinations of RTH samples in the all-taxa and diatom data sets showed that algal assemblages were more related to physical habitat characteristics and the presence of grazers than to the urban gradient (Table 8). The all-taxa ordination extracted more variability

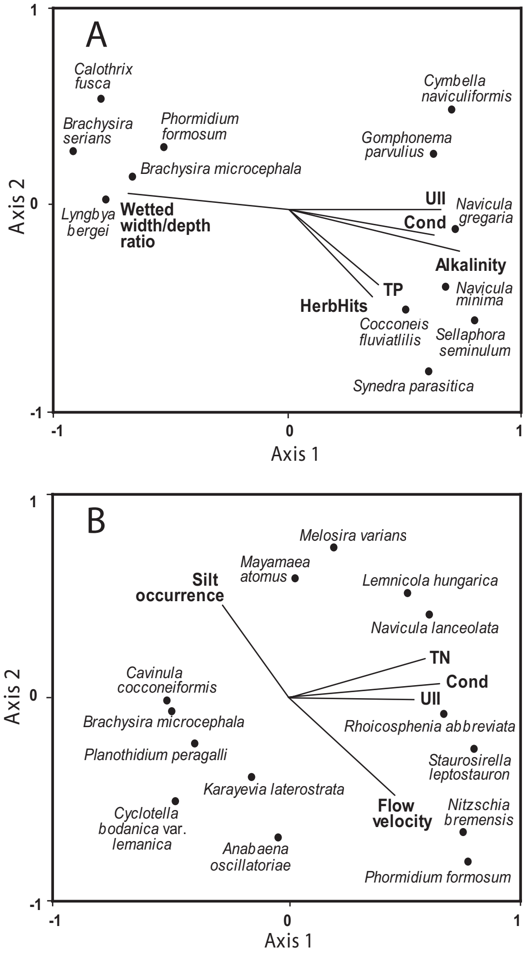

FIGURE 4. Results of nonmetric multidimensional scaling ordinations for (A) RTH and (B) DTH samples from 30 streams in the Boston study area. Joint plots of species and environmental variables were obtained by rotating ordinations to align the UII variable with the first ordination axis. Abbreviations for variables are listed in Table 1.

of species data (86%) than the diatom ordination (77%). The ordination axis aligned with the UII extracted only a low amount of variation of species data—21% in the all-taxa data set and 19% in the diatom data set. The relatively short line for the UII (Figure 5A), corresponding to its low correlation with ordination (Table 8), indicated that this variable was not associated with considerable variation in the assemblage composition. Variation of algal assemblages along the gradient of urban intensity was associated mostly with hydrological variables, such as frequency of stream level (stage) above or below particular values (Table 8). Positive correlation between stage-related characteristics and the UII-aligned axis indicated that streams were more flashy in urban settings than in nonurban settings and that this factor could cause shifts in the composition of algal assemblages along the urban gradient. Abundance of invertebrate scrapers and herbivorous fish were important factors in ordination of the all-taxa data set but not in the diatom data set (Table 8), indicating that grazers may exert a selective pressure on particular nondiatom taxa, most probably macroscopic algae. Abundance of the largescale stoneroller was positively correlated and abundance of invertebrate scrapers was negatively correlated with the UII-aligned axis; therefore, these variables could be associated with algal assemblage composition along the urban gradient. Other variables that had strong correlations with ordination but were not associated with urbanization gradient were several characteristics of channel morphology and canopy closure.

Ordination of DTH samples indicated that assemblages in soft sediments were more strongly related to the urban intensity gradient than assemblages on rocks (Table 9). Ordinations of the all-taxa and diatom data sets accounted for 83% and 75% of variability in species data, respectively. The axis aligned with the UII extracted 36% and 39% of the variation of the all-taxa and diatom ordinations, respectively. The UII variable in both ordinations was associated with the highest amount of variability in the species data compared to all other measured variables (Table 9). Other variables that had highest correlations with ordination but were not strongly aligned with the UII-aligned axis were characteristics of flow regime, channel morphology and sediment composition, concentration and number of herbicide detections, water-mineral content, and nitrogen content (Table 9; Figure 5B). Algal taxa at the high end of the urban gradient were common pollution-tolerant species, such as *Navicula veneta* and *Scenedesmus acutus*, whereas some of those at the low end were taxa of limited geographic distribution (*Surirella stalagma*, *N. repentina*) that could be indicators of natural conditions in the BIR study area.

Salt Lake City study area.—The taxa with the highest relative abundances in streams of the SLC study area were the diatoms *Achnanthidium minutissimum, Amphora pediculus, Rhoicosphenia abbreviata*, and *Nitzschia inconspicua*; filamentous cyanobacteria *Homoeothrix janthina*, *Phormidium autumnale*, and *Calothrix parietina*; an unidentified coccoid cyanobacterium; and the chantransia stage of red algae. *Phormidium autumnale* had a significant negative correlation (Kendall's tau, $P < 0.05$) with the UII in the RTH sample data set. Two

TABLE 7. Correlations of environmental variables and NMS ordination axes for the DTH 30-sample data set for the Boston study area. Ordinations were rotated to maximize loadings of the first axis on the urban intensity index. Only environmental variables with highest multiple r^2 (Σr^2) are shown. Significant correlations ($P < 0.05$) are in bold. Abbreviations for variables and variable units are in Table 1.

	All taxa				Diatoms only			
Environmental variable	axis 1	axis 2	axis 3	Σr^2	axis 1	axis 2	axis 3	Σr^2
$NO_2 + NO_3$	**0.60**	0.28	0.30	0.53	**0.55**	0.12	–0.16	0.34
Conductivity	**0.66**	0.07	0.30	0.52	**0.64**	0.06	–0.15	0.43
SO_4	**0.66**	–0.22	–0.13	0.49	**0.51**	0.20	**0.37**	0.43
TN	**0.59**	0.19	0.31	0.48	**0.61**	0.11	–0.22	0.43
Mean flow velocity	**0.46**	**–0.48**	0.03	0.45	**0.52**	**0.46**	0.29	0.57
Maximum flow velocity	**0.49**	**–0.45**	0.05	0.45	**0.50**	**0.41**	0.33	0.52
Alkalinity	**0.62**	0.15	0.15	0.43	**0.71**	0.25	–0.15	0.59
Mxh95	–0.33	0.15	0.53	0.41	–0.09	–0.14	**–0.48**	0.26
Dissolved oxygen	**–0.58**	0.14	0.05	0.37	**–0.54**	–0.04	0.12	0.31
Coefficient of variation of discharge	**–0.47**	0.35	0.02	0.35	–0.23	–0.18	0.00	0.09
Channel relative roughness	**–0.50**	0.28	–0.10	0.33	**–0.62**	0.01	0.09	0.39
Coefficient of variation of flow velocity	–0.34	**0.46**	–0.06	0.33	–0.26	**–0.46**	–0.22	0.33
TP	**0.48**	0.17	0.25	0.32	**0.51**	0.11	–0.13	0.29
Discharge	**0.41**	**–0.37**	–0.06	0.31	**0.47**	0.09	0.18	0.26
Wetted width–depth ratio	**–0.52**	0.15	–0.13	0.31	**–0.68**	–0.03	0.11	0.48
Urban intensity index	**0.55**	–0.02	0.00	0.30	**0.67**	–0.02	0.00	0.45
Silt occurrence	–0.27	**0.44**	–0.15	0.29	–0.34	–0.24	–0.07	0.02
Bank-full width–depth ratio	**–0.50**	0.15	–0.10	0.28	**–0.54**	0.03	0.17	0.32
Channel shape index	**–0.49**	0.09	–0.14	0.27	**–0.64**	–0.03	0.13	0.43
Forest	**–0.50**	–0.04	0.05	0.25	**–0.58**	0.09	–0.01	0.34
Road density	**0.46**	0.06	0.02	0.22	**0.64**	–0.04	–0.05	0.41
TKN	**0.43**	0.10	0.13	0.21	**0.61**	0.10	–0.28	0.46
Population density	**0.45**	–0.04	–0.05	0.20	**0.59**	–0.12	–0.01	0.37
Wetted depth	**0.42**	–0.11	–0.01	0.19	**0.57**	–0.21	–0.11	0.39
Maximum wetted depth	**0.39**	–0.10	0.01	0.16	**0.54**	–0.25	–0.08	0.36
Coefficient of variation of bank-full width–depth	0.20	–0.02	0.32	0.14	**0.54**	0.27	–0.15	0.38
% silt + gravel	0.31	–0.04	–0.05	0.10	**0.53**	–0.19	–0.24	0.37
% sand	0.28	–0.10	–0.05	0.09	**0.53**	–0.11	–0.14	0.31
% gravel + boulder	–0.29	0.06	0.04	0.09	**–0.51**	0.19	0.23	0.35
Percentage of reach area as riffles	0.09	–0.11	–0.26	0.09	0.21	**0.50**	**0.40**	0.45
% fine	0.27	–0.05	–0.08	0.08	**0.53**	–0.19	–0.18	0.35
Number of herbicide detections	0.24	–0.01	0.12	0.07	0.40	**0.41**	–0.18	0.36

diatoms commonly associated with sandy sediments, *Amphora pediculus* and *Nitzschia inconspicua,* correlated positively with the UII.

Algal assemblages on hard substrates in urban streams of the SLC area were apparently influenced by the increased concentrations of ions and nutrients (Table 10). Both NMS ordinations of the all-taxa and diatom data sets extracted a high percentage of variability—87% and 84%, respectively. The ordination axis aligned with the UII extracted 43% of the variability in the all-taxa data set and 41% in the diatom data set. Several variables related to water-mineral content, TP, and the percentage of fine-grained sediments were positively correlated with the UII-aligned axis (Table 10). Water-mineral content could be considered the most probable cause of the shift in the algal assemblage composition along the urban gradient in the SLC. Algal taxa at the high end of the urban gradient were diatoms commonly found in waters of high ionic strength, such as *Diatoma moniliformis* and

TABLE 8. Correlations of environmental variables and NMS ordination axes for the RTH 27-sample data set from the Birmingham study area. Ordinations were rotated to maximize loadings of the first axis on the urban intensity index. Only environmental variables with highest multiple r^2 (Σr^2) are shown. Significant correlations ($P < 0.05$) are in bold. Abbreviations for variables and variable units are in Table 1.

	All taxa				Diatoms only			
Environmental variable	axis 1	axis 2	axis 3	Σr^2	axis 1	axis 2	axis 3	Σr^2
Coefficient of variation of canopy closure	0.20	0.04	**–0.64**	0.45	0.09	0.04	0.02	0.01
Canopy closure	–0.10	–0.05	**0.65**	0.44	–0.07	0.06	0.02	0.01
Dissolved oxygen	–0.07	**–0.56**	–0.28	0.39	–0.32	0.08	0.30	0.20
% silt + clay	**–0.51**	0.02	–0.34	0.38	–0.20	–0.29	0.10	0.13
Scrapers	**–0.41**	**0.40**	–0.24	0.38	–0.09	–0.35	–0.36	0.26
Mxl5	**0.61**	0.04	–0.08	0.37	0.37	**0.44**	0.07	0.33
Wetted depth	**–0.48**	0.32	–0.13	0.35	–0.03	–0.27	–0.17	0.10
Stoneroller	**0.44**	–0.37	–0.10	0.34	0.33	0.25	0.14	0.19
Channel relative roughness	**0.39**	–0.36	0.13	0.30	0.25	0.06	0.28	0.14
Flow-stability index	–0.32	0.25	–0.33	0.28	–0.27	–0.32	0.08	0.18
Maximum wetted depth	**–0.46**	0.20	–0.11	0.27	–0.13	–0.26	–0.08	0.09
Periodr7	**0.50**	0.07	0.09	0.27	**0.53**	**0.38**	–0.05	0.43
Periodr9	**0.49**	0.06	0.10	0.26	**0.50**	0.37	–0.04	0.38
Periodr5	**0.48**	0.09	0.08	0.25	**0.56**	0.36	–0.05	0.45
Segment sinuosity	–0.23	**0.43**	–0.05	0.24	–0.10	–0.36	–0.06	0.14
Periodf9	**0.45**	0.03	0.09	0.21	**0.46**	0.37	–0.04	0.35
Periodr3	**0.43**	0.01	0.15	0.21	**0.59**	0.36	–0.09	0.48
Mean basin elevation	0.29	–0.35	0.05	0.21	**–0.40**	0.30	0.02	0.25
Periodf7	**0.43**	0.01	0.09	0.19	**0.46**	0.34	–0.05	0.33
Periodf3	**0.42**	0.01	0.11	0.19	**0.52**	0.31	–0.06	0.37
Silt occurrence	0.15	0.36	0.20	0.19	0.17	–0.10	**–0.49**	0.28
Periodf1	0.10	0.31	0.18	0.14	**0.49**	0.16	**–0.47**	0.48
Coefficient of variation of bank-full width–depth ratio	0.20	–0.01	0.32	0.14	–0.16	0.13	**0.66**	0.47
Periodr1	0.04	0.32	0.16	0.13	**0.41**	0.11	–0.45	0.38
Percentage of reach area as riffles	–0.01	–0.33	0.00	0.11	–0.02	0.34	**0.51**	0.38
Urban intensity index	0.29	–0.01	–0.05	0.09	**0.52**	0.01	0.00	0.27
Basin area	0.07	0.24	0.18	0.09	**0.47**	–0.02	–0.42	0.39
Periodf5	–0.13	–0.03	–0.26	0.08	**0.49**	0.33	–0.06	0.35
Coefficient of variation of channel shape index	0.17	–0.19	0.09	0.08	0.03	0.12	**0.54**	0.30
Uplands	–0.25	–0.12	–0.08	0.08	–0.04	–0.16	**0.51**	0.28
Road density	0.22	–0.03	–0.15	0.07	**0.54**	–0.03	–0.03	0.29
Variation in wetted width	0.22	–0.10	–0.01	0.06	–0.15	0.07	**0.62**	0.42
Bank-full width	0.19	–0.13	0.00	0.05	**0.56**	–0.03	0.06	0.32
Total herbicide concentration	0.21	–0.07	0.03	0.05	**0.55**	0.06	0.01	0.30
Coefficient of variation of bank-full width	0.03	–0.14	–0.07	0.02	–0.14	–0.02	**0.60**	0.38

Encyonema auerswaldii (Figure 6A). Taxa at the low end of the urban gradient, such as *Diatoma mesodon* and *Homoeothrix janthina,* were typical inhabitants of cold, oligotrophic, and fast-flowing streams.

Ordination of DTH samples showed weaker relations of algal assemblages to the urban gradient in the SLC area (Table 11). The all-taxa and diatom ordinations extracted 84% and 85% of variance, respectively. After rotation, the first ordination axis aligned with the UII extracted 22% and 31% of variance, respectively. The all-taxa ordination was related mostly to light conditions, canopy closure, stream size

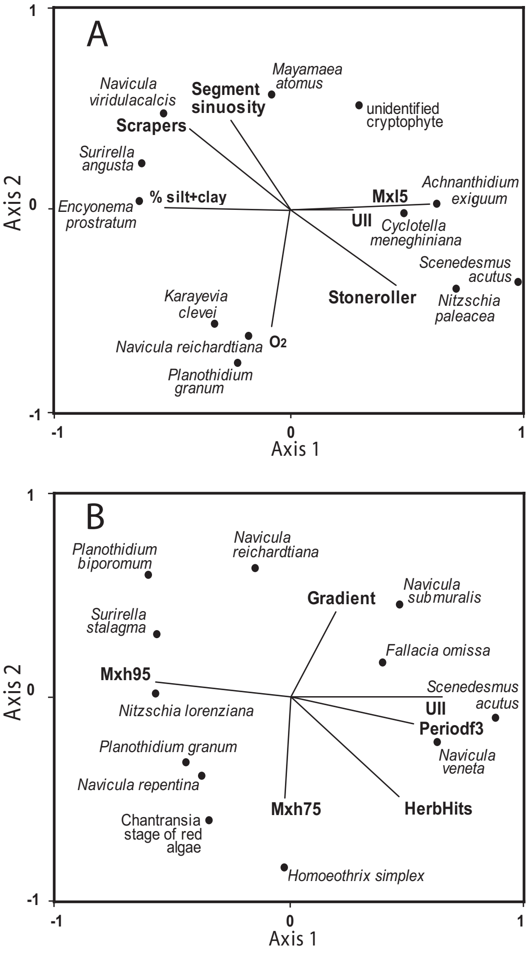

FIGURE 5. Results of nonmetric multidimensional scaling ordinations for (A) RTH and (B) DTH samples from 27 streams in the Birmingham study area. Joint plots of species and environmental variables were obtained by rotating ordinations to align the UII variable with the first ordination axis. Abbreviations for variables are listed in Table 1.

(as stream order, basin area and discharge, stream depth and width), and some chemical characteristics, such as F, pH, and NH_4. The variables most closely aligned with the UII-axis were those related to stream size and canopy closure (negative correlation) and residue on evaporation (positive correlation). Light reaching the stream bottom had a strong relation to algal assemblage structure. Light conditions generally were worse in the urban streams, despite less canopy closure, because of increased suspended sediments. Some cyanobacteria (*Calothrix parietina, Homoeothrix janthina*) and the diatom *Cocconeis neodiminuta*, which often is associated with sandy sediments, were positioned at the high end of the urban gradient (Figure 6B). Although this analysis did not indicate very strong relations between algal assemblages and stream environment, the higher concentration of dissolved solids (measured as residue on evaporation and concentrations of Na, K, Cl, SO_4, and SiO_2) was a likely factor related to the assemblage patterns revealed by this ordination. In the diatom ordination, variables related to stream size and residue on evaporation were the most important factors, but concentration of nutrients (TKN, TP, SiO_2) and some ions (Na, K, Cl, SO_4) and sediment size also had high correlations with ordination axes.

Percentages of pollution-sensitive, oligosaprobous, and oligotraphentic diatoms mostly decreased, while percentages of pollution-tolerant, α-mesosparobous + polysaprobous, and eutraphentic diatoms increased with urbanization (Table 12). This pattern was most pronounced in the BOS study area, less obvious in the SLC area, and weakest in the BIR area. Percentages of pollution-tolerant and saprophilous taxa were always higher in urban streams, although other metrics showed less consistency.

Discussion

The results of this study indicate that patterns in algal assemblages along urban intensity gradients vary regionally. Of the various attributes of algal assemblages tested, only proportions of taxa tolerant to general and organic pollution consistently tended to be higher in urban streams than in nonurban streams, although correlations of these attributes with UII were not always statistically significant. Algal biomass and diversity increased or decreased along the urban gradient depending on natural factors and human influences.

Our work demonstrates that climate and geology imposed ultimate constraints on the structure of algal assemblages in streams as predicted by the conceptual models of Biggs (1990) and Stevenson (1997). Lower algal biomass in the BOS study area in comparison to algal biomass in the SLC and BIR areas was in agreement with a generally observed pattern of lower biomass levels in streams of higher latitudes where climate is harsher and nutrients are lower compared to streams of lower latitudes (Dodds et al. 1998). Higher species diversity in the BIR area in comparison to diversity in the BOS and SLC areas confirmed previous observations that highest diversity of stream algae in the United States occurs in the warm, humid Southeast (Potapova and Charles 2004). The higher proportion of oligohalobous algal taxa in the BOS area compared to

TABLE 9. Correlations of environmental variables and NMS ordination axes for the DTH 27-sample data set from the Birmingham study area. Ordinations were rotated to maximize loadings of the first axis on the urban intensity index. Only environmental variables with highest multiple r^2 (Σr^2) are shown. Significant correlations ($P < 0.05$) are in bold. Abbreviations for variables and variable units are in Table 1.

	All taxa				Diatoms only			
Environmental variable	axis 1	axis 2	axis 3	Σr^2	axis 1	axis 2	axis 3	Σr^2
Urban intensity index	**0.65**	–0.02	–0.37	0.55	**0.71**	–0.03	0.00	0.51
Forest	**–0.62**	0.11	**0.38**	0.53	**–0.63**	0.15	0.10	0.43
Periodf3	**0.51**	–0.13	**–0.42**	0.45	**0.66**	0.04	–0.07	0.44
Periodf5	**0.50**	–0.14	**–0.42**	0.44	**0.65**	0.08	–0.05	0.43
Number of herbicide detections	**0.46**	**–0.47**	0.00	0.44	0.28	**–0.46**	–0.22	0.34
Periodr5	**0.52**	–0.12	**–0.38**	0.43	**0.65**	0.11	–0.13	0.45
Periodr3	**0.50**	–0.18	–0.37	0.42	**0.64**	0.02	–0.16	0.44
Periodf9	**0.46**	–0.15	**–0.40**	0.40	**0.62**	0.12	–0.07	0.40
Periodf7	**0.47**	–0.14	**–0.40**	0.40	**0.63**	0.11	–0.04	0.40
Periodr9	**0.47**	–0.15	**–0.38**	0.40	**0.62**	0.12	–0.09	0.40
Periodr7	**0.48**	–0.12	**–0.39**	0.39	**0.63**	0.12	–0.11	0.42
Mean basin elevation	–0.29	0.33	**–0.42**	0.36	0.13	**–0.52**	**0.54**	0.58
Mxh95	**–0.56**	0.07	0.19	0.35	**–0.53**	0.09	0.15	0.31
% cobbles	–0.34	–0.17	**–0.41**	0.32	0.13	–0.13	0.02	0.04
Stoneroller	0.22	0.18	**–0.48**	0.31	**0.63**	0.23	0.27	0.52
Mg	**0.51**	–0.17	–0.04	0.29	0.36	–0.08	–0.08	0.14
Relief	–0.26	0.36	–0.30	0.28	0.08	**0.45**	0.24	0.26
Cultivated	**–0.31**	–0.33	0.27	0.28	**–0.46**	–0.23	–0.12	0.27
Mxl5	0.12	0.07	**–0.50**	0.26	**0.46**	0.15	–0.07	0.24
Segment sinuosity	–0.05	0.07	**0.51**	0.26	–0.35	–0.26	–0.26	0.26
Mxh75	–0.02	**–0.50**	–0.05	0.25	–0.07	–0.08	–0.04	0.01
% gravel	0.13	0.22	**0.43**	0.25	**–0.41**	–0.01	–0.04	0.17
Bank-full depth	–0.03	0.07	**–0.48**	0.24	**0.53**	–0.02	–0.09	0.28
Surface-water gradient	0.21	**0.41**	–0.09	0.22	0.21	0.22	**0.41**	0.26
% silt + gravel	–0.16	0.02	0.44	0.22	**–0.58**	0.21	–0.34	0.49
Total herbicide concentration	0.27	–0.17	–0.34	0.21	**0.48**	–0.30	–0.18	0.36
Flow-stability index	0.01	0.15	**0.43**	0.21	**–0.43**	–0.24	0.00	0.24
Bank-full width	0.27	–0.05	–0.35	0.20	**0.60**	–0.18	–0.13	0.41
Wetted width	0.31	–0.08	–0.31	0.20	**0.49**	–0.29	–0.24	0.38
$NO_3 + NO_2$	0.04	–0.12	**0.43**	0.20	–0.24	**–0.41**	–0.12	0.24
Scrapers	–0.32	0.06	0.28	0.18	**–0.46**	0.01	–0.34	0.32
Discharge	0.16	0.08	0.36	0.16	–0.04	**–0.52**	–0.02	0.27
Wetted width–depth ratio	0.29	–0.03	–0.22	0.13	**0.43**	–0.14	0.21	0.24
TN	0.10	–0.08	0.31	0.12	–0.05	**–0.50**	–0.19	0.28
Basin area	0.09	–0.20	–0.23	0.10	0.25	–0.06	**–0.52**	0.33
Residue on evaporation	0.26	–0.10	0.13	0.09	0.24	**–0.44**	**–0.39**	0.40
Uplands	0.03	0.07	0.30	0.09	–0.02	**–0.48**	0.05	0.23
Conductivity	0.21	–0.06	0.08	0.05	0.23	**–0.41**	–0.37	0.35
Periodf1	0.17	–0.03	–0.04	0.03	0.19	–0.10	**–0.50**	0.30
Ca	0.10	–0.10	0.11	0.03	0.05	**–0.44**	–0.20	0.23
Dissolved oxygen	0.03	0.02	0.13	0.02	0.02	–0.06	**0.48**	0.23

the dominance of halophilic species in the two other study areas reflected differences in the bedrock composition and, therefore, in water mineralization among the study areas. Biotic interactions, such as the presence of grazers, also influenced algal assemblages. In the BIR study area, the herbivorous largescale stoneroller was able to tolerate urban-related habitat disturbance (Meador et al. 2005, this volume). The

TABLE 10. Correlations of environmental variables and NMS ordination axes for the RTH 30-sample data set from the Salt Lake City study area. Ordinations were rotated to maximize loadings of the first axis on the urban intensity index. Only environmental variables with highest multiple r^2 (Σr^2) are shown. Significant correlations ($P < 0.05$) are in bold. Abbreviations for variables and variable units are in Table 1.

	All taxa				Diatoms only			
Environmental variable	axis 1	axis 2	axis 3	Σr^2	axis 1	axis 2	axis 3	Σr^2
Na	**0.63**	0.05	0.22	0.44	**0.48**	–0.02	0.15	0.26
Cl	**0.64**	0.20	0.06	0.44	**0.51**	0.04	0.11	0.27
SiO_2	**0.59**	0.21	0.13	0.40	0.30	–0.06	–0.07	0.10
Residue on evaporation	**0.58**	0.24	–0.01	0.39	**0.55**	0.15	–0.13	0.34
Conductivity	**0.58**	0.20	–0.02	0.37	**0.58**	0.22	–0.07	0.39
K	**0.52**	–0.06	0.28	0.36	**0.40**	–0.02	0.37	0.30
% gravel + boulders	**–0.55**	–0.18	–0.05	0.34	**–0.57**	–0.10	0.19	0.37
% silt + gravel	**0.55**	0.18	0.05	0.34	**0.57**	0.10	–0.19	0.37
Mg	**0.51**	0.24	–0.13	0.34	**0.57**	0.31	–0.17	0.45
F	**0.47**	–0.21	0.25	0.32	0.21	–0.28	**0.49**	0.36
% sand	**0.55**	0.15	–0.05	0.32	0.49	–0.02	–0.12	0.25
Mean dominant substrate size	**–0.54**	–0.17	0.02	0.32	**–0.63**	–0.05	0.21	0.44
Alkalinity	**0.38**	0.34	–0.25	0.32	**0.54**	**0.44**	–0.33	0.60
% fine	**0.54**	0.17	–0.01	0.32	**0.49**	0.11	–0.15	0.27
Coefficient of variation of flow velocity	–0.28	**–0.48**	–0.10	0.32	–0.28	**–0.53**	**0.37**	0.49
Grassland	–0.45	0.27	–0.16	0.30	0.03	**0.49**	–0.03	0.24
Coefficient of variation of bank-full width	**0.39**	0.37	0.01	0.29	**–0.61**	–0.24	0.30	0.52
Ca	0.33	0.33	–0.26	0.28	**0.51**	**0.40**	**–0.42**	0.60
Bank-full width–depth ratio	–0.26	**–0.42**	–0.19	0.28	–0.39	0.21	0.17	0.23
TP	**0.49**	0.00	0.17	0.27	**0.53**	0.00	0.14	0.31
Fe	–0.16	**–0.37**	0.34	0.27	0.26	–0.27	0.03	0.14
Channel shape index	–0.34	–0.36	–0.16	0.27	**–0.48**	–0.35	**0.48**	0.59
Wetted width–depth ratio	–0.30	**–0.40**	–0.11	0.26	**–0.41**	**–0.51**	**0.56**	0.74
Segment sinuosity	0.28	0.28	0.33	0.26	**0.54**	0.28	–0.12	0.39
Urban intensity index	**0.50**	0.06	–0.07	0.26	**0.54**	0.00	0.00	0.29
Embeddedness	0.26	**0.43**	0.00	0.25	**0.61**	**0.50**	–0.33	0.73
Coefficient of variation of discharge	–0.24	**–0.43**	–0.08	0.25	–0.31	**–0.65**	**0.47**	0.73
Depth at sampling location	0.16	**0.46**	–0.22	0.25	0.09	**0.34**	–0.13	0.14
Channel relative roughness	**–0.37**	–0.33	0.08	0.25	–0.36	**–0.55**	0.32	0.53
TKN	0.25	–0.18	0.21	0.14	**0.38**	–0.15	**0.38**	0.31
Manning’s channel roughness	–0.15	–0.34	–0.04	0.14	–0.37	–0.27	0.25	0.27
Maximum wetted depth	0.08	0.35	0.00	0.13	–0.08	**0.50**	–0.24	0.32
Wetted depth	0.08	0.36	0.00	0.13	–0.06	**0.50**	–0.24	0.32
% silt + clay	0.32	0.05	–0.10	0.12	**0.44**	0.03	–0.35	0.32
Number of herbicide detections	0.16	–0.24	0.14	0.10	**0.38**	–0.13	0.42	0.33
Velocity at sampling location	0.10	0.29	0.06	0.10	–0.04	**0.39**	**–0.38**	0.30
Flow velocity	–0.04	0.25	0.18	0.09	–0.27	0.33	–0.34	0.30
Maximum flow velocity	–0.09	0.22	0.15	0.08	–0.30	0.28	–0.34	0.29
Silt occurrence	0.20	0.09	–0.07	0.05	**0.53**	0.09	0.32	0.39

presence of this grazer was not only associated with reduced algal biomass, but also with shifts in taxonomic composition and diversity of algae.

Nonuniform responses of stream algal assemblages to urbanization reflected the regional differences in human influences. The gradient of urban intensity in

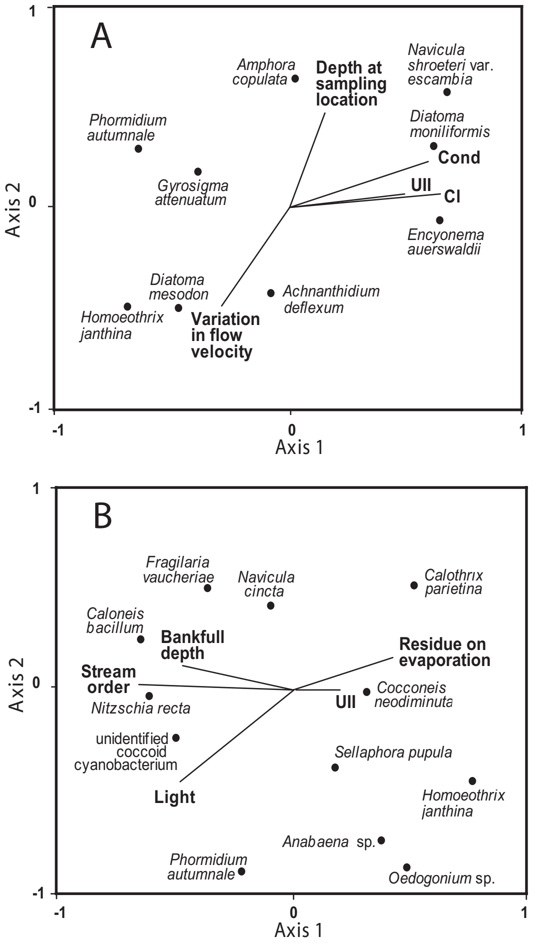

FIGURE 6. Results of nonmetric multidimensional scaling ordinations for (A) 30 RTH and (B) 28 DTH samples from streams in the Salt Lake City study area. Joint plots of species and environmental variables were obtained by rotating ordinations to align the UII variable with the first ordination axis. Abbreviations for variables are listed in Table 1.

the BOS and SLC study areas was associated mostly with the transition from natural landscapes (forest and shrub land) to urban areas. In the BIR area, not only natural landscapes, but also percentages of agricultural land decreased along an urban gradient. In agreement with this pattern, concentrations of nutrients and major ions significantly increased along gradients of urban intensity in the BOS and SLC study areas, but not in the BIR area. Presumably, agricultural inputs were replaced by urban inputs in BIR. Taxonomic composition of the stream algal assemblages changed especially along the urban gradient in the BOS and SLC study areas where water chemistry was related to urban intensity. In the BIR area, patterns of algal composition along the urban gradient were related more to physical habitat characteristics and the presence of grazers. Taxonomic composition of algal assemblages in the BOS study area showed a clear pattern along the conductivity gradient, which was collinear with the gradient of urban intensity. The process of site selection for the BOS area ensured homogeneity of natural conditions of the data set, meaning that increased conductivity at the urban sites was caused primarily by human influence. Thus, the ability of algae to indicate water-mineral content may be exploited successfully to monitor water mineralization in affected streams of the BOS area. The composition of algal assemblages also was related to water-mineral content in the SLC study area. However, urban development was concentrated in lower elevations, while nonurban sampling was conducted in higher elevations. Water-mineral content naturally increases downstream; therefore, we could not be sure that an increase in water-mineral content at the urban sites was a result of human influence alone. Abundance of halophilic diatoms on hard substrates of SLC urban streams can be considered a sign of human influences with caution only.

We found that while algal assemblages in the BOS and SLC study areas had higher biomass and diversity in urban streams than in less affected streams, assemblages in the BIR streams exhibited opposite patterns. Evidently, algae in the nonurban BOS and SLC streams were nutrient-limited, and increases in nutrient concentrations in urban streams were at least partly associated with higher algal abundance and diversity. Patterns in species composition of algal assemblages also were closely associated with nutrients. The strongest correlations occurred in the BOS area where nutrient concentrations increased significantly with urbanization. In the SLC and BIR study areas, even in the absence of strong correlations between nutrient concentrations and urban intensity, most algal taxa occurring at the upper end of the urban gradient were eutraphentic diatoms. The composition of benthic algae has potential as an indicator of nutrient concentrations in running waters (Kelly and Whitton 1995; Pan et al. 1996; Winter and Duthie 2000; Soininen and Niemelä 2002), but detailed, regional-scale studies are needed to create reliable algae-based monitoring tools. In particular, many species typical of nutrient-rich waters are broadly distributed and well known, whereas oligotraphentic species often are characteristic of more limited geographic areas and are not sufficiently studied (Potapova and Charles 2004). This may explain why, in this study, we sometimes did not observe decreases in relative abundance of

TABLE 11. Correlations of environmental variables and NMS ordination axes for the DTH 28-sample data set from the Salt Lake City study area. Ordinations were rotated to maximize loadings of the first axis on the urban intensity index. Only environmental variables with highest multiple r^2 (Σr^2) are shown. Significant correlations ($P < 0.05$) are in bold. Abbreviations for variables are in Table 1.

	All taxa				Diatoms only			
Environmental variable	axis 1	axis 2	axis 3	Σr^2	axis 1	axis 2	axis 3	Σr^2
Light	**–0.48**	**–0.48**	0.34	0.57	**–0.41**	**0.39**	0.05	0.32
Stream order	**–0.66**	0.03	–0.16	0.47	**–0.72**	–0.28	**0.53**	0.87
Grassland	**–0.65**	0.11	0.16	0.46	**–0.56**	0.00	0.37	0.44
F	**0.43**	–0.05	**–0.42**	0.36	**0.45**	0.36	–0.32	0.43
Basin area	**–0.56**	–0.03	–0.18	0.35	**–0.60**	–0.15	**0.44**	0.57
pH	–0.22	0.06	**–0.53**	0.33	–0.29	–0.11	0.29	0.18
Canopy closure	**–0.51**	–0.18	0.12	0.30	–0.19	–0.10	**0.52**	0.31
Discharge	**–0.45**	–0.04	–0.29	0.29	**–0.56**	–0.11	**0.45**	0.53
NH_4	–0.09	–0.30	**0.43**	0.28	0.14	0.28	–0.07	0.10
Uplands	–0.12	**0.45**	–0.24	0.27	0.10	0.13	0.20	0.07
Bank-full width	**–0.44**	0.06	–0.25	0.25	**–0.59**	0.01	0.25	0.41
Wetted width	**–0.42**	0.01	–0.27	0.25	**–0.59**	–0.02	0.27	0.43
Bank-full depth	**–0.45**	0.12	–0.01	0.22	–0.11	**0.39**	0.07	0.16
TKN	–0.03	–0.20	–0.37	0.18	0.16	**0.74**	0.01	0.57
Na	0.37	0.08	–0.32	0.25	**0.65**	0.30	–0.08	0.52
K	0.16	–0.12	**–0.39**	0.19	0.39	**0.58**	–0.04	0.49
Cl	0.30	0.10	–0.32	0.20	**0.62**	0.31	0.01	0.48
Residue on evaporation	**0.43**	0.15	–0.10	0.22	**0.67**	–0.09	–0.16	0.48
Velocity at sampling location	–0.30	0.19	–0.26	0.19	–0.30	–0.20	**0.50**	0.38
SiO_2	**0.42**	–0.05	–0.02	0.17	**0.62**	0.02	–0.21	0.43
Relative channel roughness	0.37	0.05	0.16	0.17	0.13	–0.01	**–0.54**	0.31
Coefficieint of variation of flow velocity	0.23	0.06	0.32	0.16	0.26	0.16	**–0.47**	0.31
SO_4	**0.38**	0.08	–0.05	0.15	**0.51**	–0.24	–0.20	0.36
Embeddedness	–0.36	–0.09	0.12	0.15	0.14	0.14	**0.53**	0.32
Wetted depth	–0.37	–0.09	0.02	0.15	**–0.39**	–0.11	0.36	0.29
Coefficient of variation of discharge	0.25	0.14	0.23	0.14	0.32	0.25	**–0.41**	0.33
Conductivity	0.26	0.20	–0.19	0.14	**0.56**	0.07	0.01	0.32
TP	0.06	–0.23	–0.28	0.13	0.34	**0.57**	0.05	0.45
Maximum wetted depth	–0.36	–0.06	0.01	0.13	**–0.40**	–0.13	0.35	0.30
Flow velocity	–0.20	–0.14	–0.23	0.11	**–0.44**	–0.27	0.27	0.34
Water temperature	0.01	–0.17	–0.21	0.07	0.19	**0.58**	0.16	0.40
Number of herbicide detections	0.22	0.04	–0.14	0.07	0.35	**0.40**	–0.30	0.37
Maximum flow velocity	–0.11	–0.13	–0.19	0.06	**–0.43**	–0.32	0.13	0.30
% silt + gravel	0.19	–0.09	0.08	0.05	**0.50**	0.21	0.10	0.31
% gravel + boulder	–0.18	0.09	–0.08	0.05	**–0.50**	–0.21	–0.11	0.31
Mean dominant substrate size	–0.11	0.01	–0.18	0.04	**0.52**	–0.20	–0.13	0.32
Urban intensity index	0.18	0.00	–0.01	0.03	**0.54**	0.00	0.00	0.29

pollution-sensitive, oligosaprobic, and oligotraphentic species along urban gradients when using metrics based on European studies.

The three study areas in this investigation also differed in the hydrological modifications to urban streams that affect patterns of flow regime along urban gradients. Dams in the watersheds of urban streams in the BOS study area stabilized discharges. Stable flow commonly promotes accumulation of algal biomass in streams (Biggs 1996), a pattern that we observed in the urban streams of the BOS study area. In contrast, urban streams in the BIR study area had more variable flow patterns.

TABLE 12. Kendall rank correlation coefficients between selected autecological diatom metrics and the urban intensity index in the three study areas. **, $P < 0.01$;*, $P < 0.05$.

Metrics	Boston		Birmingham		Salt Lake City	
	RTH	DTH	RTH	DTH	RTH	DTH
	$n = 30$	$n = 30$	$n = 27$	$n = 27$	$n = 30$	$n = 28$
Pollution-sensitive[a]	–0.50**	–0.35**	0.08	–0.08	–0.17	–0.25
Pollution-tolerant[a]	0.55**	0.27*	0.18	0.12	0.11	0.14
Oligosaprobous[b]	0.38**	–0.15	–0.17	–0.17	–0.30*	0.01
α-meso + polysaprobous[b]	0.66**	0.33**	0.18	0.11	0.44**	0.41**
Oligotraphentic[b]	0.12	–0.18	–0.15	–0.32*	–0.39**	–0.16
Eutraphentic[b]	0.42**	0.35**	0.13	–0.01	0.21	–0.06

[a] From Lange-Bertalot (1979)

[b] From van Dam et al. (1994)

Higher disturbance levels associated with stream flashiness may lower algal biomass and diversity and affect species membership (Biggs et al. 1998), as was observed in the BIR urban streams. Flow variability, measured as discharge or stage variability, may affect algal assemblages at different temporal scales (Clausen and Biggs 1997; Matthaei et al. 2003). Flow variability in the days or weeks preceding algal sampling often determines at which successional stage the algal assemblages will be found and which life forms will dominate. Long-term flow variability, measured over seasons and years, and current velocity may control the local species pool, favoring species best adapted for a particular hydrological stream type. In our study, streams were sampled within relatively short time periods in each study area and during periods of stable flow; thus, short-term flow conditions were not considered as explanatory variables in our analyses. Flow regime was quantified by using long-term stage observations and channel morphology. Stage-related variables, such as the number of periods when stage rose above or fell below specific levels, characterized urban streams in the BIR area as having a less stable flow regime than the background streams. This flow variability apparently was reflected in the composition of algal assemblages. The correlative nature of this study, however, only allows us to hypothesize about the causal relations between long-term flow regime and the composition of algal assemblages.

Our study differed fundamentally from other studies of algal assemblages in urban streams in that we used the multimetric index of urban intensity based on several infrastructure, socioeconomic, and land-use characteristics. Studying relations between biological assemblages and a general measure of human influences could be enlightening for several reasons. Various stressors associated with human influence may have a cumulative effect on biota. A single disturbance-quantifying index, such as the UII, may be used instead of the multiple characteristics of impairment once strong relations have been established among such an index, individual stressors, and biological assemblages. Our analyses demonstrated, however, that individual environmental factors associated with urbanization more often than the UII showed strong relations to algal assemblage composition, biomass, and diversity. In almost all data sets in this study, a number of proximate environmental factors had higher correlations with the NMS ordination axes than with the UII. Similarly, Sonneman et al. (2001) found that diatom communities in Australian urban streams were more strongly related to water chemistry than to a gradient of urban intensity, quantified as the proportion of impervious surface in the watershed.

Results of this study imply that no universal algae-based indicators can be used successfully in bioassessment across different geographic zones and environmental settings. The relative abundance of some taxa, recognized worldwide as reliable indicators of nutrient-rich and generally polluted or unpolluted waters, was the single attribute of algal assemblages showing the most consistent response to urbanization in this study. Our gradient analyses demonstrated, however, that a large amount of additional information on the relations between various habitat variables and algal assemblages in each area could be explored and then used in bioassessment. For instance, algal assemblages in our study showed distinct responses to many physical habitat characteristics. Further observational and experimental studies may clarify the significance of these responses and their usefulness for stream monitoring.

The design of this pilot study allowed us to compare patterns of biota along urban gradients in different environmental settings, but not to develop metrics for immediate use in bioassessment. Such work requires not only exploratory, but also confirmatory analyses and larger data sets specifically collected to investigate the effects of particular stressors on stream algal assemblages. Our work illustrated, however, the importance of developing regional-scale methods of bioassessment that are based on the detailed investigations of biological community responses to specific stresses associated with human influences.

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